

Review

Seed Priming as an Effective Technique for Enhancing Salinity Tolerance in Plants: Mechanistic Insights and Prospects for Saline Agriculture with a Special Emphasis on Halophytes

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Abstract: Seed priming is a simple, inexpensive, and effective pre-sowing technique that enables plants to better tolerate abiotic stresses, including high soil salinity, which is a major limiting factor in the establishment of halophytes for saline agriculture, as germinating seeds and early seedlings of many halophytes are sensitive compared to the mature vegetative stage. This article attempts to provide an overview of the research on the seed priming effects on halophyte seeds and subsequent seedlings/plants. Different physio-chemical and molecular processes, including the induction of priming/stress memory, which enhance salinity tolerance following seed priming, have also been discussed. This review also covers the aspects of reactive oxygen species (ROS), and nitric oxide (NO) signaling(s) that are activated as a result of seed priming. Finally, the limitations and prospects of seed priming to enhance the agronomic potential of halophytes for saline agriculture have been discussed.

Keywords: seed priming; halophyte; salinity tolerance; priming memory; signaling



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1. Introduction

Salinity is a serious agricultural problem which is being increasingly intensified due to the combined effects of global climate changes and fast expanding human population [1–3]. Rising temperatures and weather pattern shifts are leading to anomalous increase in frequency and intensity of drought and flooding, which are escalating the salinization of arable land and water resources [1,4]. Salinization on a global scale is transforming about 3 hectares of arable land into unproductive areas every minute, hence potentially reducing 10–20 million hectares of arable land to zero productivity annually [5]. It is anticipated that if current trends continue, more than half of arable land will become saline by 2050 [6]. Most plants including our major conventional crops are sensitive to even as low as 4 dS m^{−1} salinity, equivalent to 40 mM NaCl [7]. As a result, salinity adversely affects crop survival and productivity, thereby compromising food security, especially in semiarid and arid areas of the world, which constitute about one-third of the Earth's surface [8,9]. This is contradictory to achieving food security in the future, as the world's population may exceed 10 billion by 2050, requiring twice as much food as it does today [10,11]. It is therefore crucial to understand the complex interactions among climate change, salinization of lands/water, and agricultural sustainability to design effective strategies for sustainable food production and resilient agricultural systems in the world.

Since conventional crops are sensitive to salinity, it is imperative to investigate alternate approaches to ensure food security in salt-affected regions [12,13]. Plants known as halophytes are naturally salt-tolerant and can produce enormous amounts of biomass in hostile saline environments such as salt marshes, salt deserts, and coastal regions [14–16]. These remarkable plants not only endure saline environments, but can also facilitate in reclamation of saline lands, improve biodiversity, and mitigate land degradation [17,18]. Hence, cultivation of halophytes on salt-hit barren lands with brackish/saline water irrigation for food, fodder, fuel, fiber, and other economic uses appears both an ecologically and economically feasible solution to supplement demands of a burgeoning population [18–20]. By harnessing the economic potentials of halophytes, farmers of the arid–saline regions can diversify their cropping systems, enhance resilience to environmental stresses, and ultimately contribute to food security in areas plagued by salinity/aridity [18,21]. Therefore, understanding and promoting the cultivation of halophytes is essential for the success of saline agriculture and long-term sustainability of agricultural practices in arid–saline regions.

Although halophytes have a high tolerance to salinity at the growth stage, most of them have low salinity tolerance during seed germination [22]. For example, quinoa, a fast-emerging halophyte crop, can tolerate high salinity during growth but is susceptible to salinity during germination [23]. Similarly, increasing salinity decreases seed germination of a halophyte fodder candidate *Panicum turgidum* [24]. Furthermore, high salinity may also result in seed mortality in some annual dicots and grasses [22,25]. Hence, there is a need to develop techniques for improving seed germination of halophytes under high salinity.

For achieving food security particularly in harsh arid–saline regions, seed priming techniques can be used as an effective and low-cost way to enhance seed germination and salinity tolerance of halophyte crop candidates [26–29]. Seed priming is an easy cost-effective pre-sowing treatment that involves hydrating seeds to a controlled extent followed by drying with the aim to activate some of the physiological processes of germination to initiate without radicle emergence [29–31]. It provides a head-start for quick germination and vigorous seedling formation and also induces tolerance to a number of abiotic stresses, including salinity [28,32–34]. This technique is especially critical in arid–saline environments where water scarcity and soil salinity substantially hinder agricultural productivity [29,34,35]. Seed priming techniques include various methods such as hydropriming (i.e., priming with water), osmopriming (i.e., priming with osmotic agents), biopriming (i.e., priming with biological agents like rhizobacteria or fungi), and redox priming (i.e., priming involving antioxidants). Each method aims to initiate metabolic processes within the seed without causing germination, effectively preparing them for future stress conditions. The selection of these solutions depends on factors such as the type of agent used, crop species, seed quality, and the specific stress being addressed [28,36,37]. In order to meet the increasing global food demand, adopting seed priming techniques can help achieve food security in vulnerable areas, encourage sustainable agricultural production, and mitigate the effects of global climate change and soil degradation. This review article aims to present a detailed overview of various seed priming methods for halophytes, exploring their physiological and biochemical effects, advantages, and limitations, as well as the underlying mechanisms that contribute to improved tolerance in saline conditions.

2. Methodology for Literature Search

For the literature search, we employed the approach outlined in [38] with slight deviations. A number of electronic databases, namely Google Scholar, Web of Science, Crossref, ScienceDirect, and Scopus, were used for the literature search. The search was performed by using the keyword filters like “seed priming”, “seed priming, salinity tolerance”, “seed priming, halophytes”, “halophytes, salinity tolerance, carbon sequestration”, and “physio-

chemical changes, seed priming, halophyte seeds” and “molecular changes, seed priming, halophytes”, “seed priming, priming memory”, and “signaling, seed priming, halophyte”, etc. Only reviews, research articles, and book chapters as document type with a timespan option of “all years” were selected. Article titles and abstracts were manually screened to exclude irrelevant and duplicate articles. After screening the top 100 publications for each of the aforementioned keywords, we selected articles most relevant to this review. Generally, articles published during the last fifteen years were preferred. However, some older articles were also chosen, if found essential.

3. General Procedure and Types of Seed Priming

Seed priming is a pre-sowing treatment that involves immersing seeds in a suitable solution or water for a certain period of time (depending on the seeds/species) and drying them to original moisture content (on fresh weight basis) followed by brief dry storage until use (Figure 1). Concentration of priming agent solution and soakage duration may vary among species and hence needs to be optimized prior to actual experiment. Based on the type of soaking agent used, seed priming techniques can be categorized into various methods. Most common seed priming types are hydropriming, osmopriming, hormonal priming, redox priming, biopriming, nanopriming, etc. Each method has distinct mechanisms and applications, making them suitable for different crops and environmental conditions. Hydropriming involves soaking seeds in water to initiate metabolic activity while preventing germination [39]. This easy and cheap priming process allows seeds to imbibe water, softens the seed coat, and activates metabolism responsible for germination, hence making seeds ready for prompt germination and vigorous seedling formation [40,41]. Hydropriming improved seed germination and/or early seedling growth of rapeseed [42], maize [43], wheat [19], sunflower [44], and basil [45] under salinity stress. Osmopriming that involves soaking seeds in low water potential (ranging from about -1.0 to -2.0 MPa) [46] solutions of various osmotic agents (e.g., polyethylene glycol- PEG and mannitol, etc.) was effective in enhancing performance of soybean [47], spinach [48], and tomato [49]. Halopriming, which is a variant of osmopriming involving seed imbibition in salt solutions (e.g., NaCl, KCl, CaCl_2 , MgCl_2 , etc.), improves germination and/or stress tolerance of wheat [50], okra [51], rice [40], and marigold [52]. Hormonal priming with different phytohormones (e.g., gibberellins, auxins, cytokinins, etc.) was productive for wheat [53], pigeon pea [54], maize [55], and hot pepper [56]. Redox priming that involves soaking seeds in solutions of redox-active agent (e.g., hydrogen peroxide, nitric oxide/sodium nitroprusside, ascorbic acid, tocopherol, etc.) improves the performance of sunflower [57], rice [58], pea [59], and wheat [60,61]. Biopriming integrates biological agents (such as beneficial bacteria and fungi) into the priming process and was reportedly effective in barley [62], finger millet [63], wheat [64,65], and maize [66,67]. Nanopriming involves the use of nanoparticles which can facilitate the delivery of nutrients or growth regulators to seeds and stimulate metabolic processes [11,68,69]. Nanopriming improved salinity tolerance of maize [70], wheat [71], rice [72], and rapeseed [73]. Most studies on priming involve seeds of cultivated plants, and this information on halophyte seeds is limited to just a few studies [28,74–76].

SUMMARY OF SEED PRIMING PROCEDURE

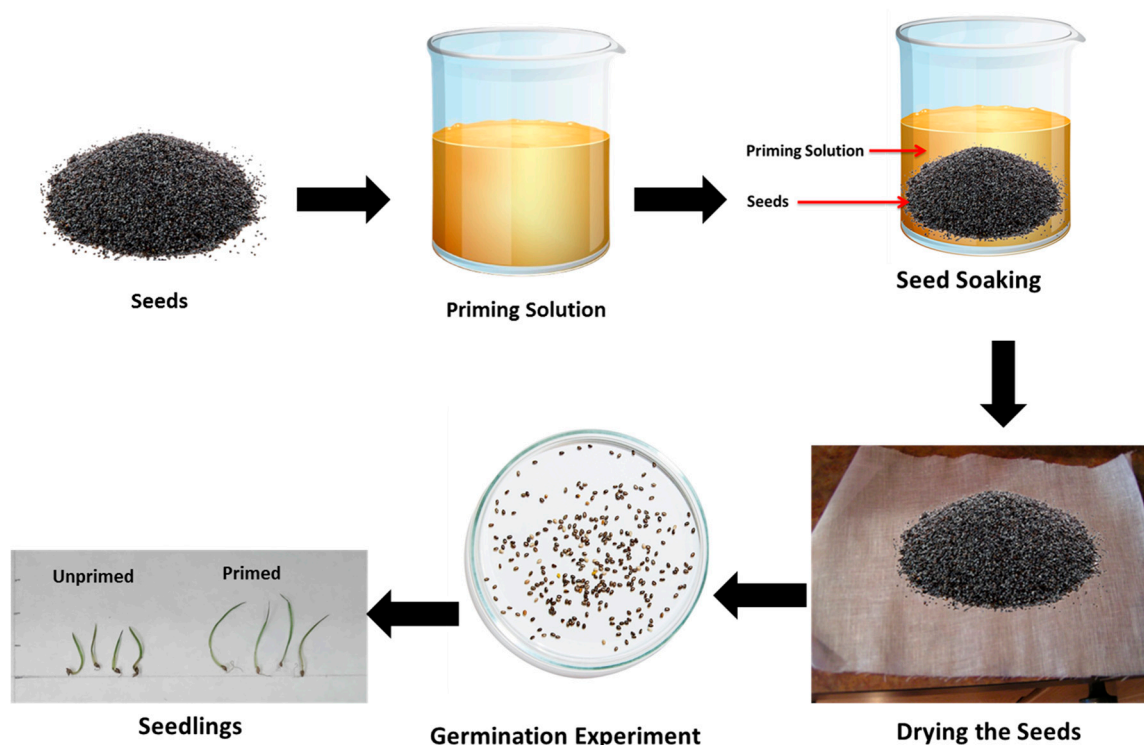


Figure 1. An outline of the seed priming procedure.

4. Seed Priming and Salinity Tolerance in Halophytes

As mentioned above, studies on efficacy of various seed priming methods on seed germination, seedling growth, and salinity tolerance of halophytes are scant ([77]; Supplementary Tables S1 and S2). Some studies have reported beneficial effects of hydro-priming on germination, growth, and salinity tolerance of halophytes. For instance, hydro-priming improved seed germination of *Atriplex canescens*, with longer (4-day) durations of hydro-priming, that resulted in higher germination percentages and rates [78]. Similarly, the 8-day hydro-priming treatment resulted in the highest germination percentage and rate of *Nitraria schoberi* seeds under 100 mM salinity and enhanced root length and biomass of seedlings [79]. Hydropriming for 12 h resulted in enhanced germination percentages in Giza02 and Q102 quinoa seeds and also improved growth parameters with higher chlorophyll content compared to unprimed control plants in salt stress conditions [80]. Meanwhile, halopriming with KNO_3 and MgSO_4 effectively mitigated the negative impacts of salinity in quinoa [80]. Similarly, seed halopriming priming with CaCl_2 , KCl , and KNO_3 enhanced germination and growth of *Hordeum maritimum* under salinity, primarily by reducing sodium ion accumulation and oxidative stress [81]. Halopriming also improved salinity tolerance of *Distichlis spicata* at low to moderate salinity levels [82]. Osmopriming seeds with low water potential solutions improved germination in salinity for *Amaranthus caudatus*, whereas osmopriming seeds with relatively higher water potential solutions was effective for *C. quinoa* [83]. Osmopriming seeds with proline enhanced germination and seedling establishment of *Cakile maritima* even at high salinity, and increases in proline and carbohydrate levels were found in the plant tissues under saline conditions compared to unprimed plants [84].

A number of studies have shown that redox priming can also improve salinity tolerance of halophytes during both seed germination and growth stages. For instance, seed priming with H_2O_2 enhanced germination (both rate and total percentage) and reduced

mean germination time of halophyte crop *Chenopodium quinoa* with concomitant stimulation in amylase activity, increased starch breakdown, enhanced amino acid and protein content following exposure to salinity [85]. Seed priming with H₂O₂ and sodium nitroprusside (SNP, a nitric oxide donor) effectively overcame primary dormancy that enhanced seed germination of an annual halophyte *Zygophyllum simplex* in moderate- and high-salinity conditions compared to unprimed control, hydropriming, and other redox priming treatments [20]. Seed priming with H₂O₂ ameliorated growth and antioxidant activities of *Cakile maritima* and *Eutrema salsugineum* under drought and salinity [74]. Likewise, H₂O₂ priming improved performance of *Crithmum maritimum* under salinity [86]. In addition, Khan et al. [87] reported that seed priming with antioxidant ascorbic acid (AsA) enhanced germination of *Suaeda fruticosa* and *Atriplex stocksii* but not of *Arthrocnemum macrostachyum*, *Haloxylon stocksii*, *Desmostachya bipinnata*, and *Aeluropus lagopoides* under saline conditions. Hence, redox priming efficacy could be species- and chemical-specific, warranting more studies in this area.

A large number of studies have been conducted in the recent past on isolation and characterization of salt-tolerant plant-growth-promoting rhizobacteria (ST-PGPRs) and fungi from the roots/root zones of halophytes and their utilization as bio-priming agents for improving the salinity tolerance of crops [88–90]. However, studies on bio-priming effects on seed germination, seedling growth, and salinity tolerance of halophytes are actually scant. Fahad and Sohaib [91] reported that the seeds of *Chenopodium quinoa* treated with *Pseudomonas* spp. displayed 100% germination in sand surface and no salinity, whereas seeds treated with *Azotobacter* spp. alone and in combination with *Azospirillum* spp. and/or *Pseudomonas* spp. resulted in a better germination response at high salinity. More studies are therefore required to unveil efficacy and underlying mechanisms of bio-priming in halophytes.

Nanopriming that involves soaking seeds in solutions of nanoparticles has been used in a number of studies for improving salinity tolerance of crops [62,69,71,92]. Many studies have also used halophyte plants for the green synthesis of nanoparticles with potential as a seed priming agent and improving salinity tolerance of crop plants [93–95]. However, little is known about nanopriming effects on seed germination and salinity tolerance of halophytes. Recently, Ashraf Ganjouii et al. [96] reported that nanopriming with selenium nanoparticles can improve growth and morphological parameters of *C. quinoa* plants under salinity stress at low concentrations. Lack of information thus warrants detailed studies on halophytes.

5. Comparative Analysis of Seed Priming Techniques

The efficacy of various seed priming strategies may vary across species, priming agents, and doses/duration. For instance, halopriming with KNO₃, hormonal priming with GA₃, and halopriming with MgSO₄ effectively mitigated the negative impacts of salinity in *C. quinoa* compared to hydropriming and CaCl₂ halopriming treatments [80]. Seed priming with halo-priming CaCl₂, KCl, and KNO₃ improved *H. maritimum* germination and growth under salt stress by reducing sodium ion accumulation and oxidative stress. Seed halopriming priming with CaCl₂ was the most effective, followed by KNO₃, and priming with KCl was the least effective in improving germination and growth of *H. maritimum* under salt stress [81]. Priming with SNP and H₂O₂ resulted in more significant improvement in seed germination under saline conditions than the AsA priming in annual halophyte *Z. simplex* [20]. In addition, hydropriming resulted in only marginal improvement in some germination and seedling growth attributes of *Z. simplex* in comparison to redox priming treatments [20]. The dose of priming also influences the beneficial effects of seed priming. For instance, osmopriming seeds with low water potential solutions

led to improved germination of *A. caudatus* seeds under salinity; however, for the seed of *C. quinoa*, hydropriming and osmopriming seeds with high water potential solutions was effective [83]. Hussain et al. [28] reported that the low (5 and 100 μ M) concentrations of melatonin (MT) were most effective as priming agents in improving seed dormancy, germination, and early seedling growth of five warm subtropical halophytes under saline conditions. Under non-saline conditions, all MT doses improved germination of *S. fruticosa* following longer (34 h) priming duration, whereas only low (5 and 100 μ M) MT doses improved germination of *Portulaca oleracea* seeds only after short (12 h) priming [28]. In the context described above, identifying the optimal balance of these factors specific to each halophytic species appears important for enhancing seed germination and seedling establishment in saline environments.

6. Mechanistic Insights: Physiochemical and Molecular Footprints

6.1. Physio-Chemical Changes

Priming induces a number of physiological, biochemical, and molecular changes in the seeds and subsequent seedlings, which enable them to efficiently deal with stressful conditions (Figure 2). However, most of the mechanistic information about seed priming is based on glycophytic crops, whereas this information on halophytes is virtually absent. Priming treatments improve hydration ability of seeds by reducing imbibition and lag phases of water absorption upon sowing [56]. The swelling of the embryo in primed seeds accelerates germination by facilitating water absorption and priming also reduces endosperm resistance [97,98]. Nagarajan et al. [99] suggested that improved seed hydration following priming was due to reorganization of seed moisture, changes in seed water-binding properties, and increasing macromolecular hydration water for germination-related metabolic activities. Dry primed seeds showed tissue detachment in X-ray photographs, which improved water flow and tissue hydration by creating free space between the cotyledons and radicle [100]. Similarly, Liu et al. [101] also noticed occurrence of free space around embryo of the dry-primed tomato seeds. Osmopriming increased hydrolysis of the endosperm tissue of *Cucumis melo* seeds [102] and also decreased endosperm mechanical resistance on the elongating tomato embryo by increasing endo- β -mannanase activity in tomato embryos [98]. Reorganization of the cytoskeleton is also essential for higher cell elongation rates and radicle protrusion. Rapeseed showed increased β -tubulin protein accumulation during PEG treatment and subsequent germination, along with increased expression of γ - and β -tubulins genes [103].

Priming treatments also improve mitochondrial and energy-related activities of the seeds [104–106]. Priming enhances ATP synthesis and ATP/ADP ratio during imbibition, with the stimulatory effect increasing with longer duration of osmotic treatment. Priming had a positive effect on tomato seeds by stimulating energy metabolism. The highest improvement occurred when the ATP/ADP ratio and energy charge (EC) were greater than about 0.75 and 1.7, respectively [107]. Seed priming also increases the number of mitochondria, as found in embryonic cells of osmoprimed leek seeds [108]. Osmopriming up-regulated expression of mitochondrial biogenesis genes in *Brassica napus* seeds, including mitochondrial ribosomal protein, EF2 elongation factor, and TIM10 and TIM23-1 translocases [103].

Priming treatments also improved phyto-hormone balance of the seeds. For instance, CaCl_2 osmopriming improved the hormonal balance of two spring wheat (*Triticum aestivum*) cultivars by way of reducing abscisic acid (ABA) concentrations and increasing salicylic acid concentrations in the MH-97 cultivar and increasing free indoleacetic and indolebutyric acid content in the Inqlab-91 cultivar [109]. Additionally, there was a strong correlation between the effectiveness of priming and ACC (1-aminocyclopropane-1-carboxylic acid)-dependent

ethylene production in sunflower seeds [104]. Several phytohormones, including zeatin, indole-3-acetic acid, and 1-aminocyclopropane carboxylic acid, showed a strong correlation with *PsMAPK2* expression in pea seeds pre-treated with H_2O_2 [59]. Nakaune et al. [110] suggested that the beneficial effect of NaCl priming on tomato seed germination was linked to an increase in the GA_4 content via GA biosynthetic gene activation and a subsequent increase in the expression of genes related to endosperm cap weakening. Seed priming significantly improved GA_3 contents in rice seeds by up-regulating the expression of *OsGA3ox1* and *OsGA20ox1* and decreased the ABA content and the expression of *OsNCED1* [111]. Similarly, NaCl osmopriming of tomato seeds up-regulated the expression of GA-biosynthesis genes GA 20-oxidase (*GA20ox*), GA 3-oxidase (*GA3ox*), and GA_4 (*GA 3beta-hydroxylase*) under salinity stress [112]. GA synthesis induced the mobilization of stored seed reserves, particularly starch which is essential for energy generation in germinating seeds and subsequent nascent seedlings. For instance, Nie et al. [111] reported enhanced starch degradation ability in primed rice seeds due to GA-mediated α -amylase expression. Same authors also reported an increase in total soluble sugar content in primed seeds. Another study found that primed true seeds of sugar beet had 0.5–4% more soluble sugar and 1.9–11.5 times higher amylase activity compared to control seeds [113].

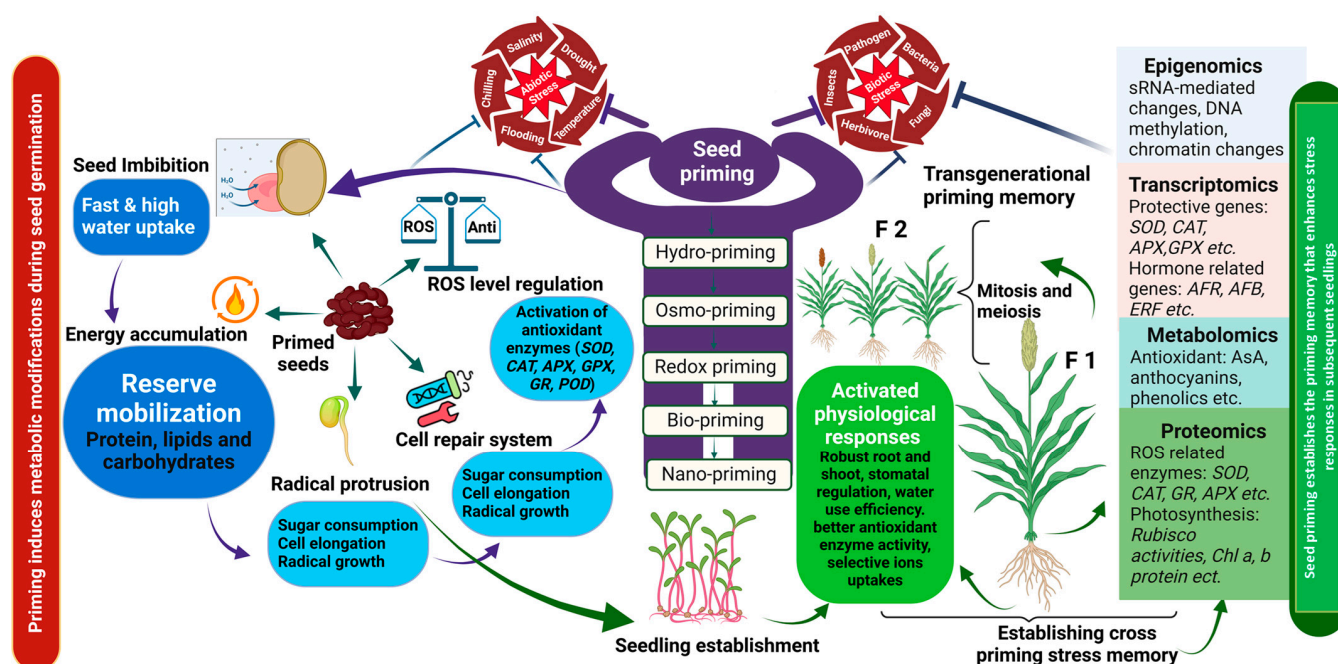


Figure 2. Summary of the mechanistic basis of beneficial effects of seed priming on seed germination and nascent seedlings.

Often, primed seeds appear to have higher levels of the osmo-protectant substances. For instance, pre-sowing treatment of *Cajanus cajan* seeds with KNO_3 or $CaCl_2$ enhanced protein, free amino acid, and soluble sugar contents during germination under salt stress [114]. The accumulation of osmotically active solutes like amino acids, ammonium compounds, and sugars was also reported in a number of species during priming, which supports seed germination under water stress [60,115–117]. Likewise, choline osmopriming enhanced salinity tolerance of wheat by increasing glycinebetaine accumulation [118].

Seed priming also reduced salinity-induced oxidative damages in primed seeds and subsequent seedlings by stimulating their antioxidant defense system. For example, salicylic acid primed seeds of *Vicia faba* showed enhanced catalase, peroxidase, ascorbate peroxidase, and glutathione reductase activities under salinity stress [119]. Similarly, various priming treatments increased the activities of antioxidant enzymes [100,110,120,121]

and contents of antioxidant compounds [120–122]. Hence, primed seeds and/or subsequent seedlings showed lower malondialdehyde (MDA, a common indicator of oxidative membrane damage) accumulation under salinity [34,70,123].

An enhanced/efficient nutrient uptake and utilization was also evident under salinity stress following seed priming. For instance, enhanced salinity tolerance of wheat after choline priming coincided with maintained beneficial elements (K^+ and Ca^{2+}) and lower toxic elements (Na^+ and Cl^-), alongside higher glycinebetaine accumulation [118]. Similarly, priming of *V. faba* seeds with melatonin augmented beneficial elements (K^+ and Ca^{2+}) levels and their ratios compared with Na^+ (i.e., K^+/Na^+ and Ca^{2+}/Na^+) in the plant leaves under salinity [124]. Bioprimering of wheat seeds with beneficial fungus *Trichoderma harzianum* enhanced agronomic nitrogen use efficiency by 3.36% under 1/4th nitrogen along with regular phosphorus and potassium levels [125].

Seed priming is also known to stimulate photosynthetic performance in the primed seedlings. For example, seedlings of *V. faba* developed from melatonin-primed seeds had more photosynthetic pigments compared to unprimed control [124]. Recently, Hussain et al. [28] reported a greater level of photosynthetic pigments in seedlings of some warm subtropical halophytes developed from melatonin-primed seeds. Seed preconditioning increased photosynthetic capacity in adult hexaploid wheat plants subjected to salt [126]. Melatonin priming improved leaf photosynthetic efficiency by stimulating Pn, Gs, Ci, Tr, and chlorophyll contents under salinity in cotton seedlings [127]. Redox priming with H_2O_2 increased Fv/Fm, transpiration, and carboxylation efficiency under salinity in *Zea mays* plants [128].

6.2. Molecular Changes

Seed priming induces a series of molecular level changes that prepare the seeds for subsequent growth. For instance, a number of germination-related and stress-responsive genes are up-regulated alongside down-regulation of dormancy-inducing and stress-sensitive genes [111,112,129]. A prominent increase in the expression of cell-cycle and DNA repair-related genes can be seen in primed seeds. Flow cytometry-based studies have revealed that DNA replication is initiated in the radicle tip cells during the osmopriming of tomato seeds [130,131]. Beginning with a 3-day incubation period in PEG, the 4C DNA signal in root tip cells of tomato enhanced and remained unaltered when the seeds were dried back to their original moisture content [132]. Interestingly, priming treatment requires at least 5% oxygen to stimulate germination, which is equivalent to the oxygen concentration needed for DNA replication [131] and hence signifies the importance of DNA replication for priming. Osmopriming of *B. napus* seeds increased the expression of various proteins, including cell division control protein 48 homolog C, cyclin P4;1, cyclin-related protein, topoisomerase II, and proliferating-cell nuclear antigen 2 [103]. The study also reported increased expression of microtubule-associated proteins, tubulin subunits, and kinesin family proteins in *B. napus* seeds during and after osmopriming. Sivritepe and Dourado [133] reported that priming facilitates the repair of chromosomal damage aged pea seeds. Priming stimulated the expression of 952 genes and 75 proteins in *B. napus*, which are required for seed germination and the start of transcriptional activity for DNA replication, repair, and cell cycle regulation [103]. In addition, Varier et al. [134] suggested that DNA damage repair occurs in primed seeds before replication primarily through DNA synthesis. This DNA damage repair is essential in enhancing seed physiological quality [135].

Seed priming also influences gene expression of germination/dormancy-related phyto-hormones. For example, seed priming significantly up-regulated the expression of *OsGA3ox1* and *OsGA20ox1* and decreased the expression of *OsNCED1*-related ABA content in rice seeds [111]. Hormonal priming with ethephon (i.e., a source of ethylene)

increased ethylene concentration and up-regulated ethylene signaling genes like *OsACS1* and *OsEIN2* [136].

Membrane proteins called aquaporins, which are specialized water channels, facilitate water movement across membranes. Kubala et al. [103] reported for *B. napus* seeds that osmopriming increased the expression of two genes encoding tonoplast aquaporins (*TIP4.1* and *TIP1.2*), with *TIP1.2* expression increasing 20-fold during post-priming germination. Similarly, the aquaporin gene expression levels were higher in the primed rice seeds than in the control seeds after 24 h of imbibition [137]. Primed seeds of *Spinacia oleracea* also showed higher expression of aquaporin coding genes, namely *SoPIP1;1*, *SoPIP2;1*, and *SoδTIP* that coincided with their greater drought tolerance compared to unprimed seeds [138].

Late embryogenesis-abundant (LEA) proteins play an important role in protecting cellular structures and macromolecules during dehydration by preventing protein inactivation, aggregation, and membrane loss. In *B. oleracea*, transcripts of *Em6* (encoding LEA group 1 protein) and *RAB18* (encoding responsive to ABA 18 protein of LEA group 2) genes were found to decrease during osmopriming, re-accumulate following slow-drying, and degrade again during seed germination [139]. Similarly, after soaking in PEG solution, *LEA4-1* and *LEA4-5* transcripts and LEA3 protein accumulated in *B. napus* [103].

Transcriptional profiling of maize seeds nano-primed with silver nanoparticles showed 140 up-regulated and 242 down-regulated differentially expressed genes (DEGs). A number of up-regulated DEGs were related to mitogen-activated protein kinase signaling pathways, hormone signal transduction, receptor-like kinases (RLKs), and many stress transcription factors (especially WRKY, MYB, NAC) [140]. A total of 221 DEGs were observed in *Silene sendtneri* seeds after seed priming with silicic acid, among which 117 genes were unique to silicic acid-primed seeds and 102 to non-primed seeds [141]. In contrast, over 1300 genes in *Medicago truncatula* were differently regulated upon PEG osmopriming at -1.7 MPa [142]. In addition, a proteomics study reported accumulation of 18 proteins in seeds of sugarbeet after hydropriming [143].

A number of recent studies have shown that seed priming can also induce epigenetic modifications, which result in heritable changes in gene expression [144–147]. These modifications do not alter the DNA sequence but instead involve chemical alterations to the DNA (e.g., methylation) or the histone proteins wrapping the DNA strands [147]. Epigenetic variations are inherited via meiosis and mitosis [148]. Hence, epigenetic changes, due to their heritable nature, may act as a “memory” for plants, enabling them to “remember” the stress conditions they experienced during seed development, equipping them with adaptability to cope with similar challenges in their early growth stages [147]. Despite several reports indicating the trans-generational inheritance potential of priming, few studies have actually investigated the role of stability in epigenetic change transmission through generations.

7. ROS and NO as Potential Signaling Cues of Seed Priming

Although little is known, ROS and NO have gained significant attention as signaling molecules following seed priming. The ROS, which have conventionally viewed as harmful byproducts of cellular metabolism, play a paradoxical role in regulating various plant processes including regulation of dormancy/germination and stress tolerance by acting as signaling molecules [149,150]. Hydrogen peroxide (H_2O_2 , a common ROS) signaling regulated seed germination in ZnO = nanoprimed *T. aestivum* seeds and improved plant performance under drought stress [151]. Similarly, priming seeds with low levels of H_2O_2 also reportedly stimulated the expression of stress-responsive genes and enhanced seed vigor and germination in crops [122,152] as well as halophytes [20,74]. Nitric oxide (NO) is another important versatile signaling agent in plants that interacts with ROS and

various hormonal pathways to promote seedling growth and stress tolerance [153,154]. Magneto-priming stimulated NO synthesis to modulate phyto-hormones, which improves soybean seed germination under salt stress [155]. Another study reported that magneto-priming enhances salt stress tolerance in soybean seedlings through an NR-dependent NO production pathway, with NO donor promoting germination and NO inhibitor inhibiting it [156]. The interaction of these signaling molecules and phytohormones produces a finely tuned response of seeds/plants to environmental cues. However, little is known about key cross-talks, fine details, and downstream molecular targets of these signaling species in primed seeds, particularly of non-crops such as halophytes.

8. Limitations and Applications of Seed Priming in Saline Agriculture

Seed priming is an effective seed enhancement approach that increases stress tolerance of seeds and subsequent seedlings under saline conditions, making it an important strategy for ensuring future food security. However, currently, there are a few limitations in its large-scale applications. For instance, some priming procedures may increase the contamination chance of the medium by microorganisms, which could significantly impede consequent seed germination [157]. Some researchers have reported that primed seeds have shorter longevity than unprimed seeds [158–160]. In a worst-case scenario, priming-induced benefits may disappear after only 14 days of storage, leading to inferior seedling performance compared to unprimed seeds [161]. However, many studies based on classical long-term storage strategies found that priming may not always reduce longevity [158]. Ma et al. [162] found that treating seeds of perennial grass *Leymus chinensis* with GA₃ significantly improved seed germination and plant growth, with a growth-promoting effect lasting for at least two years. Initial financial investment in adopting seed priming such as for acquiring priming agents, equipment, and storage facility cannot be overlooked, especially for small-holder farmers with tight budgets [163]. To overcome these challenges, further research, optimization of priming methods, and practical training and resources are needed. Most studies on seed priming approaches focus on seeds and young seedlings under controlled conditions, but information about the seedling and adult plant performance under natural environments is unclear, necessitating urgent focus on mature plants developed from the primed seeds, particularly at the reproductive phase, to evaluate long-term effects on various life cycle stages. Our understanding about epigenetic factors influencing “priming memory” duration following seed priming is far from comprehensive. Hence, research in this domain is needed to establish “long-term-primed” plants, enhance stress tolerance, and improve crop productivity for future food security. Another important challenge is the variability in response among different plant species and even among varieties within the same species, making it difficult to implement a one-size-fits-all approach. Last but not least, our understanding of seed priming techniques and underlying mechanisms is mostly based on crops, with little information available regarding halophytes, particularly those with crop potential. Yet, the advantages of seed priming may outweigh the disadvantages. However, further research, optimization of priming methods, and practical training for farmers are crucial to overcome the shortcomings of current priming protocols for securing food supplies and enhancing saline agriculture in the face of global challenges. Global warming and climate changes are causing a decrease in precipitation and water quality, forcing farmers to utilize brackish/saline water for irrigation. Since most crops are sensitive to salinity, utilization of halophytes that can withstand high salinity levels appears a sustainable solution for future agriculture. However, despite high tolerance at the growth stage, the sensitivity of germinating seeds and nascent seedlings could be a bottleneck in the success of halophyte-based saline agriculture in the future. Seed priming, in this context, could be a game-changer for enhanced establishment and productivity of

halophytes in stressful barren areas. Nonetheless, more focused research is required to fill the aforementioned gaps and technical hurdles.

9. Conclusions

Seed priming is an easy, low-cost, and effective approach to improve salinity tolerance of early sensitive life-cycle stages of plants including the halophytes, which are the plants naturally found in saline environments. This treatment triggers a number of physiological, biochemical, and molecular changes in seeds, leading to faster germination, improved seedling establishment, and increased resilience under salinity. However, challenges include optimizing priming parameters for different species, reducing seed viability post-priming, and finding cost-effective methods for large-scale agricultural applications. Despite these obstacles, seed priming has significant potential in halophyte cultivation, thereby contributing to sustainable farming practices in degraded saline/dry lands.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/seeds4010014/s1>, Table S1. Effects of seed priming on germination related parameters of halophytes in salinity-based experiments; Table S2. Effects of seed priming on growth and physio-chemical parameters of halophytes in salinity-based experiments.

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References

1. Singh, A. Soil Salinity: A Global Threat to Sustainable Development. *Soil Use Manag.* **2022**, *38*, 39–67. [[CrossRef](#)]
2. Tarolli, P.; Luo, J.; Park, E.; Barcaccia, G.; Masin, R. Soil Salinization in Agriculture: Mitigation and Adaptation Strategies Combining Nature-Based Solutions and Bioengineering. *iScience* **2024**, *27*, 108830. [[CrossRef](#)] [[PubMed](#)]
3. Oelviani, R.; Adiyoga, W.; Bakti, I.G.M.Y.; Suhendrata, T.; Malik, A.; Chanifah, C.; Samijan, S.; Sahara, D.; Sutanto, H.A.; Wulanjari, M.E.; et al. Climate Change Driving Salinity: An Overview of Vulnerabilities, Adaptations, and Challenges for Indonesian. *Agric. Weather Clim. Soc.* **2023**, *16*, 29–49. [[CrossRef](#)]
4. Corwin, D.L. Climate Change Impacts on Soil Salinity in Agricultural Areas. *Eur. J. Soil Sci* **2021**, *72*, 842–862. [[CrossRef](#)]
5. Bridges, E.M.; Oldeman, L.R. Global Assessment of Human-Induced Soil Degradation. *Arid Soil Res. Rehabil.* **1999**, *13*, 319–325. [[CrossRef](#)]
6. Butcher, K.; Wick, A.F.; DeSutter, T.; Chatterjee, A.; Harmon, J. Soil Salinity: A Threat to Global Food Security. *Agron. J.* **2016**, *108*, 2189–2200. [[CrossRef](#)]
7. Munns, R.; Tester, M. Mechanisms of Salinity Tolerance. *Annu. Rev. Plant Biol.* **2008**, *59*, 651–681. [[CrossRef](#)]
8. Golla, B. Agricultural Production System in Arid and Semi-Arid Regions. *Int. J. Agric. Sci. Food technol.* **2021**, *7*, 234–244.
9. Aksoy, S.; Yildirim, A.; Gorji, T.; Hamzeshpour, N.; Tanik, A.; Sertel, E. Assessing the Performance of Machine Learning Algorithms for Soil Salinity Mapping in Google Earth Engine Platform Using Sentinel-2A and Landsat-8 OLI Data. *Adv. Space Res.* **2022**, *69*, 1072–1086. [[CrossRef](#)]
10. Nadathur, S.; Wanasundara, P.; Scanlin, L. Feeding the Globe Nutritious Food in 2050: Obligations and Ethical Choices. In *Sustainable Protein Sources Advances for a Healthier Tomorrow*; Nadathur, S., Scanlin, L., Wanasundara, P., Eds.; Elsevier: Amsterdam, The Netherlands, 2024; pp. 649–668. [[CrossRef](#)]

11. Ghosh, A.; Kumar, A.; Biswas, G. Exponential Population Growth and Global Food Security: Challenges and Alternatives. In *Bioremediation of Emerging Contaminants from Soils: Soil Health Conservation for Improved Ecology and Food Security*; Kumar, P., Srivastav, A.L., Chaudhary, V., Hullebusch, E.D., Busquets, R., Eds.; Elsevier: Amsterdam, The Netherlands, 2024; pp. 1–20. [\[CrossRef\]](#)
12. Siegel, F.R. Food 2050: More Mouths to Feed—Food Availability and Access. In *The Earth's Human Carrying Capacity: Limitations Assessed, Solutions Proposed*; Siegel, F.R., Ed.; Springer International Publishing: Cham, Switzerland, 2021; pp. 87–107. [\[CrossRef\]](#)
13. Grigore, M.N.; Vicente, O. Wild Halophytes: Tools for Understanding Salt Tolerance Mechanisms of Plants and for Adapting Agriculture to Climate Change. *Plants* **2023**, *12*, 221. [\[CrossRef\]](#)
14. Flowers, T.J.; Colmer, T.D. Salinity Tolerance in Halophytes. *New Phytol.* **2008**, *179*, 945–963. [\[CrossRef\]](#) [\[PubMed\]](#)
15. Flowers, T.J.; Galal, H.K.; Bromham, L. Evolution of Halophytes: Multiple Origins of Salt Tolerance in Land Plants. *Funct. Plant Biol.* **2010**, *37*, 604–612. [\[CrossRef\]](#)
16. Hameed, A.; Khan, M.A. Halophytes: Biology and economic potentials. *Karachi Univ. J. Sci.* **2011**, *39*, 40–44.
17. Qadir, M.; Tubeileh, A.; Akhtar, J.; Larbi, A.; Minhas, P.S.; Khan, M.A. Productivity Enhancement of Salt-Affected Environments through Crop Diversification. *Land Degrad. Dev.* **2008**, *19*, 429–453. [\[CrossRef\]](#)
18. Panta, S.; Flowers, T.; Lane, P.; Doyle, R.; Haros, G.; Shabala, S. Halophyte Agriculture: Success Stories. *Environ. Exp. Bot.* **2014**, *107*, 71–83. [\[CrossRef\]](#)
19. Mirza, S.R.; Ilyas, N.; Batool, N. Seed Priming Enhanced Seed Germination Traits of Wheat under Water, Salt and Heat Stress. *Pure Appl. Biol.* **2021**, *4*, 650–658. [\[CrossRef\]](#)
20. Hussain, S.; Nisar, F.; Bhatt, A.; Nielsen, B.L.; Gul, B.; Hameed, A. Redox Priming Alleviates Dormancy and Improves Salinity Tolerance of Seeds and Seedlings of Medicinal Halophyte *Zygophyllum simplex* L. *Appl. Res. Med. Aromat. Plants* **2022**, *30*, 100384. [\[CrossRef\]](#)
21. Hameed, A.; Hussain, S.; Rasheed, A.; Ahmed, M.Z.; Abbas, S. Exploring the Potentials of Halophytes in Addressing Climate Change-Related Issues: A Synthesis of Their Biological, Environmental, and Socioeconomic Aspects. *World* **2024**, *5*, 36–57. [\[CrossRef\]](#)
22. Gul, B.; Ansari, R.; Flowers, T.J.; Khan, M.A. Germination Strategies of Halophyte Seeds under Salinity. *Environ. Exp. Bot.* **2013**, *92*, 4–18. [\[CrossRef\]](#)
23. Schabes, F.I.; Sigstad, E.E. Calorimetric Studies of Quinoa (*Chenopodium quinoa* Willd.) Seed Germination under Saline Stress Conditions. *Thermochim. Acta* **2005**, *428*, 71–75. [\[CrossRef\]](#)
24. Al-Khateeb, S.A. Effect of Salinity and Temperature on Germination, Growth and Ion Relations of *Panicum turgidum* Forssk. *Bioresour. Technol.* **2006**, *97*, 292–298. [\[CrossRef\]](#) [\[PubMed\]](#)
25. Hameed, A.; Ahmed, M.; Gulzar, S.; Gul, B.; Alam, J.; Hegazy, A.; Alatar, A.; Khan, M.A. Seed germination and recovery responses of suaeda heterophylla to abiotic stresses. *Pak. J. Bot.* **2013**, *45*, 1649–1656. [\[CrossRef\]](#)
26. Amir, M.; Prasad, D.; Khan, F.A.; Khan, A.; Ahmad, B.; Astha, A. Seed Priming: An Overview of Techniques, Mechanisms, and Applications. *Plant Sci. Today* **2024**, *11*, 553–563. [\[CrossRef\]](#)
27. Hernández, J.A.; Barba-Espín, G.; Díaz-Vivancos, P. Seed Priming Technology: Current Perspectives. *Seeds* **2024**, *3*, 540–543. [\[CrossRef\]](#)
28. Hussain, S.; Nisar, F.; Gul, B.; Hameed, A. Seed Priming with Melatonin Improved Salinity Tolerance of Halophytes during Early Life-Cycle Stages. *Plant Growth Regul.* **2024**, *103*, 351–368. [\[CrossRef\]](#)
29. Jarrar, H.; El-Keblawy, A.; Albawab, M.; Ghenai, C.; Sheteiwy, M. Seed Priming as a Promising Technique for Sustainable Restoration of Dryland. *Restor. Ecol.* **2024**, *32*, e14182. [\[CrossRef\]](#)
30. Johnson, R.; Puthur, J.T. Seed Priming as a Cost Effective Technique for Developing Plants with Cross Tolerance to Salinity Stress. *Plant Physiol. Biochem.* **2021**, *162*, 247–257. [\[CrossRef\]](#) [\[PubMed\]](#)
31. Diya, A.; Beena, R.; Jayalekshmy, V.G. Physiological, Biochemical and Molecular Mechanisms of Seed Priming: A Review. *Legume Res. Int. J.* **2024**, *47*, 159–166. [\[CrossRef\]](#)
32. Ibrahim, E.A. Seed Priming to Alleviate Salinity Stress in Germinating Seeds. *J. Plant Physiol.* **2016**, *192*, 38–46. [\[CrossRef\]](#)
33. Tamindžić, G.; Ignjatov, M.; Miljković, D.; Červenski, J.; Milošević, D.; Nikolić, Z.; Vasiljević, S. Seed Priming Treatments to Improve Heat Stress Tolerance of Garden Pea (*Pisum sativum* L.). *Agriculture* **2023**, *13*, 439. [\[CrossRef\]](#)
34. Zhang, H.; Zhang, X.; Gao, G.; Ali, I.; Wu, X.; Tang, M.; Chen, L.; Jiang, L.; Liang, T. Effects of Various Seed Priming on Morphological, Physiological, and Biochemical Traits of Rice under Chilling Stress. *Front. Plant Sci.* **2023**, *14*, 1146285. [\[CrossRef\]](#) [\[PubMed\]](#)
35. Devika, O.S.; Singh, S.; Sarkar, D.; Barnwal, P.; Suman, J.; Rakshit, A. Seed Priming: A Potential Supplement in Integrated Resource Management Under Fragile Intensive Ecosystems. *Front. Sustain. Food Syst.* **2021**, *5*, 654001. [\[CrossRef\]](#)
36. Wang, J.; Tao, M.; Xu, L.; Fan, N.; Zhao, C.; Xiao, Z.; Wang, Z. Chitosan Nanocarriers Loaded with Salicylic Acid for Controlling Fall Armyworm (*Spodoptera frugiperda*) and Alleviating Oxidative Stress in Maize Plants. *Environ. Sci. Nano* **2023**, *10*, 3295–3306. [\[CrossRef\]](#)

37. Tripathi, D.K.; Bhat, J.A.; Antoniou, C.; Kandhol, N.; Singh, V.P.; Fernie, A.R.; Fotopoulos, V. Redox Regulation by Priming Agents Toward a Sustainable Agriculture. *Plant Cell Physiol.* **2024**, *65*, 1087–1102. [\[CrossRef\]](#)
38. Khondoker, M.; Mandal, S.; Gurav, R.; Hwang, S. Freshwater Shortage, Salinity Increase, and Global Food Production: A Need for Sustainable Irrigation Water Desalination—A Scoping Review. *Earth* **2023**, *4*, 223–240. [\[CrossRef\]](#)
39. Sumbal, S.; Ali, A.; Nasser Binjawhar, D.; Ullah, Z.; Eldin, S.M.; Iqbal, R.; Sher, H.; Ali, I. Comparative Effects of Hydropriming and Iron Priming on Germination and Seedling Morphophysiological Attributes of Stay-Green Wheat. *ACS Omega* **2023**, *8*, 23078–23088. [\[CrossRef\]](#) [\[PubMed\]](#)
40. Jisha, K.C.; Puthur, J.T. Seed Halopriming Outdo Hydropriming in Enhancing Seedling Vigor and Osmotic Stress Tolerance Potential of Rice Varieties. *J. Crop Sci. Biotechnol.* **2014**, *17*, 209–219. [\[CrossRef\]](#)
41. Jiang, B.; Wang, L.; Xu, C.; Yan, M. Hydropriming Enhances the Germination of Aged Ultra-Dry Wheat Seeds. *Seed Sci. Technol.* **2020**, *48*, 57–63. [\[CrossRef\]](#)
42. Mosavian, S.N.; Esmailzade-Moridani, M. Effect of Hydro-Priming Duration on Germination and Early Seedling Growth of Rapeseed under Salinity Stress. *Afr. J. Agric. Res.* **2016**, *11*, 4395–4400. [\[CrossRef\]](#)
43. Akter, L.; Fakir, O.A.; Alam, M.K.; Islam, M.U.; Chakraborti, P.; Alam, M.J.; Rashid, M.H.; Begum, M.; Kader, M.A. Amelioration of Salinity Stress in Maize Seed Germination and Seedling Growth Attributes through Seed Priming. *Open J. Soil Sci.* **2018**, *8*, 137–146. [\[CrossRef\]](#)
44. Matias, J.R.; Torres, S.B.; Leal, C.C.P.; Leite, M.D.S.; Carvalho, S.M.C. Hydropriming as Inducer of Salinity Tolerance in Sunflower Seeds. *Rev. Bras. Eng. Agríc. Ambient.* **2018**, *22*, 255–260. [\[CrossRef\]](#)
45. Farahani, H.A.; Maroufi, K. Effect of Hydropriming on Seedling Vigour in Basil (*Ocimum basilicum* L.) under Salinity Conditions. *Adv. Environ. Biol.* **2011**, *5*, 828–834.
46. Corbineau, F.; Taskiran-Özbingöl, N.; El-Maarouf-Bouteau, H. Improvement of Seed Quality by Priming: Concept and Biological Basis. *Seeds* **2023**, *2*, 101–115. [\[CrossRef\]](#)
47. Sadeghi, H.; Khazaei, F.; Yari, L.; Sheidaei, S. Effect of seed osmopriming on seed germination behavior and vigor of soybean (*Glycine max* L.). *J. Agric. Biol. Sci.* **2011**, *6*, 39–43.
48. Chen, K.; Arora, R. Dynamics of the Antioxidant System during Seed Osmopriming, Post-Priming Germination, and Seedling Establishment in Spinach (*Spinacia oleracea*). *Plant Sci.* **2011**, *180*, 212–220. [\[CrossRef\]](#)
49. Mauromicale, G.; Cavallaro, V. Effects of Seed Osmopriming on Germination of Tomato at Different Water Potential. *Seed Sci. Technol.* **1995**, *23*, 393–403.
50. Hamidi, R.; Pirasteh-Anosheh, H.; Izadi, M. Effect of Seed Halo-Priming Compared with Hydro-Priming on Wheat Germination and Growth. *Intl. J. Agron. Plant Prod.* **2013**, *4*, 1611–1615.
51. Tania, S.S.; Rhaman, M.S.; Hossain, M.M. Hydro-Priming and Halo-Priming Improve Seed Germination, Yield and Yield Contributing Characters of Okra (*Abelmoschus esculentus* L.). *Trop. Plant Res.* **2020**, *7*, 86–93. [\[CrossRef\]](#)
52. Afzal, I.; Ashraf, S.; Qasim, M.; Basra, S.M.A.; Shahid, M. Does Halopriming Improve Germination and Seedling Vigour in Marigold (*Tagetes* spp.). *Seed Sci. Technol.* **2009**, *37*, 436–445. [\[CrossRef\]](#)
53. Ulfat, A.; Majid, S.A.; Hameed, A. Hormonal seed Priming Improves Wheat (*Triticum aestivum* L.) Field Performance under Drought and Non-stress Conditions. *Pak. J. Bot.* **2017**, *49*, 1239–1253.
54. Sneideris, L.C.; Gavassi, M.A.; Campos, M.L.; D’Amico-Damião, V.; Carvalho, R.F. Effects of Hormonal Priming on Seed Germination of Pigeon Pea under Cadmium Stress. *An. Acad. Bras. Cienc.* **2015**, *87*, 1847–1852. [\[CrossRef\]](#) [\[PubMed\]](#)
55. Afzal, I.; Noor, M.A.; Bakhtavar, M.A.; Ahmad, A.; Haq, Z. Improvement of Spring Maize Performance through Physical and Physiological Seed Enhancements. *Seed Sci. Technol.* **2015**, *43*, 238–249. [\[CrossRef\]](#)
56. Khan, H.A.; Pervez, M.A.; Ayub, C.M.; Ziaf, K.; Balal, R.M.; Shahid, M.A.; Akhtar, N. Hormonal Priming Alleviates Salt Stress in Hot Pepper (*Capsicum annuum* L.). *Soil Environ.* **2009**, *28*, 130–135.
57. Silva, P.C.C.; Azevedo Neto, A.D.D.; Gheyi, H.R.; Ribas, R.F.; Silva, C.R.D.R.; Cova, A.M.W. Salt Tolerance Induced by Hydrogen Peroxide Priming on Seed Is Related to Improvement of Ion Homeostasis and Antioxidative Defense in Sunflower Plants. *J. Plant Nutr.* **2021**, *44*, 1207–1221. [\[CrossRef\]](#)
58. Hemalatha, G.; Renugadevi, J.; Eevera, T. Studies on Seed Priming with Hydrogen Peroxide for Mitigating Salt Stress in Rice. *Int. J. Curr. Microbiol. Appl. Sci.* **2017**, *6*, 691–695. [\[CrossRef\]](#)
59. Barba-Espín, G.; Hernández, J.A.; Diaz-Vivancos, P. Role of H₂O₂ in Pea Seed Germination. *Plant Signal. Behav.* **2012**, *7*, 193–195. [\[CrossRef\]](#)
60. Farooq, M.; Irfan, M.; Aziz, T.; Ahmad, I.; Cheema, S.A. Seed Priming with Ascorbic Acid Improves Drought Resistance of Wheat. *J. Agron. Crop Sci.* **2013**, *199*, 12–22. [\[CrossRef\]](#)
61. Shah, T.; Latif, S.; Khan, H.; Munsif, F.; Nie, L. Ascorbic Acid Priming Enhances Seed Germination and Seedling Growth of Winter Wheat under Low Temperature Due to Late Sowing in Pakistan. *Agronomy* **2019**, *9*, 757. [\[CrossRef\]](#)

62. Khan, I.; Lubna; Asaf, S.; Bilal, S.; Alamri, S.S.; Jan, R.; Asif, S.; Kim, K.M.; AL-Harrasi, A. Enhanced Growth and Stress Tolerance in Barley (*Hordeum vulgare*) through Biopriming with *Aspergillus Niger* CSR3: A Promising Approach for Sustainable Agriculture in Saline Environments. *Cereal Res. Commun.* **2024**, *52*, 1201–1213. [\[CrossRef\]](#)
63. Rawat, L.; Bisht, T.S.; Kukreti, A. Potential of Seed Biopriming with *Trichoderma* in Ameliorating Salinity Stress and Providing Resistance against Leaf Blast Disease in Finger Millet (*Eleusine coracana* L.). *Indian Phytopathol.* **2022**, *75*, 147–164. [\[CrossRef\]](#)
64. Dief, H.E.S.; Hashem, E.S.A.; Fawzan, S.; El-Sayed, A.S.A. Alleviation of Salt Stress in *Triticum aestivum* by Biopriming with *Phanerochaete chrysosporium*. *J. Crop Sci. Biotechnol.* **2021**, *24*, 103–116. [\[CrossRef\]](#)
65. Hadj Brahim, A.; Ben Ali, M.; Daoud, L.; Jlidi, M.; Akremi, I.; Hmani, H.; Feto, N.A.; Ben Ali, M. Biopriming of Durum Wheat Seeds with Endophytic Diazotrophic Bacteria Enhances Tolerance to *Fusarium* Head Blight and Salinity. *Microorganisms* **2022**, *10*, 970. [\[CrossRef\]](#)
66. Singh, S.; Singh, U.B.; Trivedi, M.; Sahu, P.K.; Paul, S.; Paul, D.; Saxena, A.K. Seed Biopriming with Salt-Tolerant Endophytic *Pseudomonas Geniculata*-Modulated Biochemical Responses Provide Ecological Fitness in Maize (*Zea mays* L.) Grown in Saline Sodic Soil. *Int. J. Environ. Res. Public Health* **2020**, *17*, 253. [\[CrossRef\]](#) [\[PubMed\]](#)
67. Iqbal, A.; Arshad, U.; Ayub, S.; Jabeen, A.; Saeed, M. Bio-Priming of Seed with *Trichoderma* sp. and *Bacillus* sp. Leads to Improved Morpho-Physiological Parameters Related to Drought Tolerance in Maize. *J. Integr. Plant Biol.* **2023**, *1*, 43–51. [\[CrossRef\]](#)
68. Nile, S.H.; Thiruvengadam, M.; Wang, Y.; Samynathan, R.; Shariati, M.A.; Rebezov, M.; Nile, A.; Sun, M.; Venkidasamy, B.; Xiao, J.; et al. Nano-Priming as Emerging Seed Priming Technology for Sustainable Agriculture—Recent Developments and Future Perspectives. *J. Nanobiotechnol.* **2022**, *20*, 254. [\[CrossRef\]](#) [\[PubMed\]](#)
69. Singh, K.M.; Baksi, S.; Rani, S.; Jha, A.B.; Dubey, R.S.; Sharma, P. NanoBoost: Maximizing Crop Resilience and Yield via Nanopriming Under Salt Stress. *Environ. Exp. Bot.* **2024**, *226*, 105937. [\[CrossRef\]](#)
70. Shah, T.; Latif, S.; Saeed, F.; Ali, I.; Ullah, S.; Abdullah Alsahli, A.; Jan, S.; Ahmad, P. Seed Priming with Titanium Dioxide Nanoparticles Enhances Seed Vigor, Leaf Water Status, and Antioxidant Enzyme Activities in Maize (*Zea mays* L.) under Salinity Stress. *J. King Saud Univ. Sci.* **2021**, *33*, 101207. [\[CrossRef\]](#)
71. Farooq, T.; Akram, M.N.; Hameed, A.; Ahmed, T.; Hameed, A. Nanopriming-Mediated Memory Imprints Reduce Salt Toxicity in Wheat Seedlings by Modulating Physiobiochemical Attributes. *BMC Plant Biol.* **2022**, *22*, 540. [\[CrossRef\]](#) [\[PubMed\]](#)
72. Soni, A.T.; Rookes, J.E.; Arya, S.S. Chitosan Nanoparticles as Seed Priming Agents to Alleviate Salinity Stress in Rice (*Oryza sativa* L.) Seedlings. *Polysaccharides* **2023**, *4*, 129–141. [\[CrossRef\]](#)
73. El-Badri, A.M.A.; Batool, M.; Mohamed, I.A.A.; Khatab, A.; Sherif, A.; Wang, Z.; Salah, A.; Nishawy, E.; Ayaad, M.; Kuai, J.; et al. Modulation of Salinity Impact on Early Seedling Stage via Nano-Priming Application of Zinc Oxide on Rapeseed (*Brassica napus* L.). *Plant Physiol. Biochem.* **2021**, *166*, 376–392. [\[CrossRef\]](#)
74. Ellouzi, H.; Sghayar, S.; Abdelly, C. H₂O₂ Seed Priming Improves Tolerance to Salinity; Drought and Their Combined Effect More than Mannitol in *Cakile Maritima* When Compared to *Eutrema salsugineum*. *J. Plant Physiol.* **2017**, *210*, 38–50. [\[CrossRef\]](#) [\[PubMed\]](#)
75. Zammali, I.; Dabbous, A.; Youssef, S.; Ben Hamed, K. Effects of Chemical Priming on the Germination of the Ornamental Halophyte *Lobularia maritima* under NaCl Salinity. *Seeds* **2022**, *1*, 99–109. [\[CrossRef\]](#)
76. Ramírez, E.; Chaâbene, Z.; Hernández-Apaolaza, L.; Rekik, M.; Elleuch, A.; de la Fuente, V. Seed Priming to Optimize Germination in *Arthrocnemum Moq.* *BMC Plant Biol.* **2022**, *22*, 527. [\[CrossRef\]](#)
77. Sghaier-Hammami, B.; Baazaoui, N.; Hammami, S.B.M.; Abdelly, C. Priming-Mediated Tolerance to Biotic and Abiotic Stresses in Halophytes. In *Handbook of Halophytes: From Molecules to Ecosystems Towards Biosaline Agriculture*; Grigore, M.N., Ed.; Springer International Publishing: Cham, Switzerland, 2020; pp. 1–26. [\[CrossRef\]](#)
78. Khaleghi, G. Investigating the Effect of Hydropriming on Germination Components of Atriplex Plant (*Atriplex canescens*) under Salinity Stress. *Greenh. Plant Prod. J.* **2024**, *1*, 47–54. [\[CrossRef\]](#)
79. Khaleghi, G. The Effect of Hydropriming on Germination Characteristics and Seedling Growth of *Nitraria Schoberi* Seeds under Salinity Stress. *Greenh. Plant Prod. J.* **2024**, *1*, 38–46. [\[CrossRef\]](#)
80. Lallouche, B.; Kouider, B.H. Effects of Hydropriming, Halopriming, and Hormopriming Seed Treatments on the Subsequent Salt Stress Tolerance of Quinoa (*Chenopodium quinoa* Willd.) in Algeria. *Acta Sci. Pol. Hortoru.* **2024**, *23*, 59–70. [\[CrossRef\]](#)
81. Ben Youssef, R.; Jelali, N.; Boukari, N.; Albacete, A.; Martinez, C.; Alfocsa, F.P.; Abdelly, C. The Efficiency of Different Priming Agents for Improving Germination and Early Seedling Growth of Local Tunisian Barley under Salinity Stress. *Plants* **2021**, *10*, 2264. [\[CrossRef\]](#) [\[PubMed\]](#)
82. Shiri, M.; Rabhi, M.; El Amrani, A.; Abdelly, C. Cross-Tolerance to Abiotic Stresses in Halophytes: Application for Phytoremediation of Organic Pollutants. *Acta Physiol. Plant.* **2015**, *37*, 209. [\[CrossRef\]](#)
83. Moreno, C.; Seal, C.E.; Papenbrock, J. Seed Priming Improves Germination in Saline Conditions for *Chenopodium quinoa* and *Amaranthus caudatus*. *J. Agron. Crop Sci.* **2018**, *204*, 40–48. [\[CrossRef\]](#)
84. Messedi, D.; Hmidi, D.; Farhani, F.; Zribi, F.; Zorrig, W.; Abdelly, C.; Debez, A. Proline Priming: An Efficient Strategy to Mitigate Salinity Impact at Early Developmental Stages of the Oilseed Halophyte *Cakile Maritima*. *Not. Bot. Horti Agrobot. Cluj-Napoca* **2024**, *52*, 13458. [\[CrossRef\]](#)

85. Hajhashemi, S.; Skalicky, M.; Brestic, M.; Pavla, V. Cross-Talk between Nitric Oxide, Hydrogen Peroxide and Calcium in Salt-Stressed *Chenopodium quinoa* Willd. At Seed Germination Stage. *Plant Physiol. Biochem.* **2020**, *154*, 657–664. [\[CrossRef\]](#)
86. Nimac, A.; Lazarević, B.; Petek, M.; Vidak, M.; Šatović, Z.; Carović-Stanko, K. Effects of Salinity and Seed Priming on Germination of Sea Fennel (*Crithmum maritimum* L.). *Agric. Conspec. Sci.* **2018**, *83*, 181–185.
87. Khan, M.A.; Ahmed, M.Z.; Hameed, A. Effect of Sea Salt and L-Ascorbic Acid on the Seed Germination of Halophytes. *J. Arid Environ.* **2006**, *67*, 535–540. [\[CrossRef\]](#)
88. Aizaz, M.; Ahmad, W.; Asaf, S.; Khan, I.; Saad Jan, S.; Salim Alamri, S.; Bilal, S.; Jan, R.; Kim, K.M.; Al-Harrasi, A. Characterization of the Seed Biopriming, Plant Growth-Promoting and Salinity-Ameliorating Potential of Halophilic Fungi Isolated from Hypersaline Habitats. *Int. J. Mol. Sci.* **2023**, *24*, 4904. [\[CrossRef\]](#) [\[PubMed\]](#)
89. Dutta, B.; Datta, A.; Dey, A.; Ghosh, A.K.; Bandopadhyay, R. Establishment of Seed Biopriming in Salt Stress Mitigation of Rice Plants by Mangrove Derived *Bacillus* sp. *Biocatal. Agric. Biotechnol.* **2023**, *48*, 102626. [\[CrossRef\]](#)
90. Meinzer, M.; Ahmad, N.; Nielsen, B.L. Halophilic Plant-Associated Bacteria with Plant-Growth-Promoting Potential. *Microorganisms* **2023**, *11*, 2910. [\[CrossRef\]](#)
91. Al-Barakah, F.N.I.; Sohaib, M. Evaluating the Germination Response of *Chenopodium quinoa* Seeds to Bacterial Inoculation under Different Germination Media and Salinity Conditions. *Seed Sci. Technol.* **2019**, *47*, 161–169. [\[CrossRef\]](#)
92. Lee, J.H.J.; Kasote, D.M. Nano-Priming for Inducing Salinity Tolerance, Disease Resistance, Yield Attributes, and Alleviating Heavy Metal Toxicity in Plants. *Plants* **2024**, *13*, 446. [\[CrossRef\]](#)
93. Munir, N.; Hanif, M.; Dias, D.A.; Abideen, Z. The Role of Halophytic Nanoparticles towards the Remediation of Degraded and Saline Agricultural Lands. *Environ. Sci. Pollut. Res.* **2021**, *28*, 60383–60405. [\[CrossRef\]](#)
94. Hanif, M.; Munir, N.; Abideen, Z.; Dias, D.A.; Hessini, K.; El-Keblawy, A. Enhancing Tomato Plant Growth in a Saline Environment through the Eco-Friendly Synthesis and Optimization of Nanoparticles Derived from Halophytic Sources. *Environ. Sci. Pollut. Res.* **2023**, *30*, 118830–118854. [\[CrossRef\]](#)
95. Ramzan, M.; Parveen, M.; Naz, G.; Sharif, H.M.A.; Nazim, M.; Aslam, S.; Hussain, A.; Rahimi, M.; Alamer, K.H. Enhancing Physio-Biochemical Characteristics in Okra Genotypes through Seed Priming with Biogenic Zinc Oxide Nanoparticles Synthesized from Halophytic Plant Extracts. *Sci. Rep.* **2024**, *14*, 23753. [\[CrossRef\]](#)
96. Ashraf Ganjouii, F.; Nasibi, F.; Manoochehri Kalantari, K.; Ahmadi Mousavi, E. Effect of Seed Priming with Selenium Nanoparticles and Plant Growth Promoting Rhizobacteria on Improving *Quinoa* Seedling Growth under Salinity Stress. *J. Plant Process Funct.* **2023**, *11*, 65–74.
97. Elouaer, M.A.; Hannachi, C. Seed Priming to Improve Germination and Seedling Growth of Safflower (*Carthamus tinctorius*) under Salt Stress. *Eurasia J. Biosci.* **2012**, *6*, 76–84. [\[CrossRef\]](#)
98. Toorop, P.E.; van Aelst, A.C.; Hilhorst, H.W.M. Endosperm Cap Weakening and Endo- β -Mannanase Activity during Priming of Tomato (*Lycopersicon esculentum* Cv. Moneymaker) Seeds Are Initiated upon Crossing a Threshold Water Potential. *Seed Sci. Res.* **1998**, *8*, 483–492. [\[CrossRef\]](#)
99. Nagarajan, S.; Pandita, V.K.; Joshi, D.K.; Sinha, J.P.; Modi, B.S. Characterization of Water Status in Primed Seeds of Tomato (*Lycopersicon esculentum* Mill.) by Sorption Properties and NMR Relaxation Times. *Seed Sci. Res.* **2005**, *15*, 99–111. [\[CrossRef\]](#)
100. Galhaut, L.; de Lespinay, A.; Walker, D.J.; Bernal, M.P.; Correal, E.; Lutts, S. Seed Priming of *Trifolium Repens* L. Improved Germination and Early Seedling Growth on Heavy Metal-Contaminated Soil. *Water Air Soil Pollut.* **2014**, *225*, 1905. [\[CrossRef\]](#)
101. Liu, Y.; van der Burg, W.J.; Aartse, J.W.; van Zwol, R.A.; Jalink, H.; Bino, R.J. X-Ray Studies on Changes in Embryo and Endosperm Morphology during Priming and Imbibition of Tomato Seeds. *Seed Sci. Res.* **1993**, *3*, 171–178. [\[CrossRef\]](#)
102. Oluoch, M.O.; Welbaum, G.E. Viability and Vigor of Osmotically Primed Muskmelon Seeds After Nine Years of Storage. *JASHS* **1996**, *121*, 408–413. [\[CrossRef\]](#)
103. Kubala, S.; Garnczarska, M.; Wojtyła, Ł.; Clippe, A.; Kosmala, A.; Żmieniecki, A.; Lutts, S.; Quinet, M. Deciphering Priming-Induced Improvement of Rapeseed (*Brassica napus* L.) Germination through an Integrated Transcriptomic and Proteomic Approach. *Plant Sci.* **2015**, *231*, 94–113. [\[CrossRef\]](#)
104. Chojnowski, M.; Corbineau, F.; Côme, D. Physiological and Biochemical Changes Induced in Sunflower Seeds by Osmopriming and Subsequent Drying, Storage and Aging. *Seed Sci. Res.* **1997**, *7*, 323–332. [\[CrossRef\]](#)
105. Dahal, P.; Kim, N.S.; Bradford, K.J. Respiration and Germination Rates of Tomato Seeds at Suboptimal Temperatures and Reduced Water Potentials. *J. Exp. Bot.* **1996**, *47*, 941–947. [\[CrossRef\]](#)
106. Ozbingol, N.; Corbineau, F.; Côme, D. Responses of Tomato Seeds to Osmoconditioning as Related to Temperature and Oxygen. *Seed Sci. Res.* **1998**, *8*, 377–384. [\[CrossRef\]](#)
107. Corbineau, F.; Özbingöl, N.; Vinel, D.; Côme, D. Improvement of Tomato Seed Germination by Osmopriming as Related to Energy Metabolism. In *Seed Biology: Advances and Applications. Proceedings of the Sixth International Workshop on Seeds, Merida, Mexico, 1999*; CABI Books: Wallingford, UK, 2000; pp. 467–476. [\[CrossRef\]](#)
108. Ashraf, M.; Bray, C.M. DNA Synthesis in Osmoprimed Leek (*Allium porrum* L.) Seeds and Evidence for Repair and Replication. *Seed Sci. Res.* **1993**, *3*, 15–23. [\[CrossRef\]](#)

109. Iqbal, M.; Ashraf, M.; Jamil, A.; Ur-Rehman, S. Does Seed Priming Induce Changes in the Levels of Some Endogenous Plant Hormones in Hexaploid Wheat Plants Under Salt Stress? *J. Integr. Plant Biol.* **2006**, *48*, 181–189. [\[CrossRef\]](#)
110. Nakaune, M.; Hanada, A.; Yin, Y.G.; Matsukura, C.; Yamaguchi, S.; Ezura, H. Molecular and Physiological Dissection of Enhanced Seed Germination Using Short-Term Low-Concentration Salt Seed Priming in Tomato. *Plant Physiol. Biochem.* **2012**, *52*, 28–37. [\[CrossRef\]](#)
111. Nie, L.; Song, S.; Yin, Q.; Zhao, T.; Liu, H.; He, A.; Wang, W. Enhancement in Seed Priming-Induced Starch Degradation of Rice Seed Under Chilling Stress via GA-Mediated α -Amylase Expression. *Rice* **2022**, *15*, 19. [\[CrossRef\]](#) [\[PubMed\]](#)
112. Elkholy, S.F.; Almutairi, Z.M. Effect of Priming With Gibberellin On Germination and Expression of Ga Biosynthesis Gene Of Tomato (*Solanum lycopersicum* L.) Seedlings Under Salt Stress. *Int. J. Bio-Technol. Res.* **2018**, *8*, 11–22. [\[CrossRef\]](#)
113. Mukasa, Y.; Takahashi, H.; Taguchi, K.; Ogata, N.; Okazaki, K.; Tanaka, M. Accumulation of Soluble Sugar in True Seeds by Priming of Sugar Beet Seeds and the Effects of Priming on Growth and Yield of Drilled Plants. *Plant Prod. Sci.* **2003**, *6*, 74–82. [\[CrossRef\]](#)
114. Verma, J.; Srivastava, A.K. Physiological Basis of Salt Stress Resistance in Pigeon Pea (*Cajanus cajan* L.). Pre-sowing seed soaking treatment in regulating early seedling metabolism during seed germination. *Plant Physiol. Biochem.* **1998**, *25*, 89–94.
115. Li, X.; Zhang, L. SA and PEG-Induced Priming for Water Stress Tolerance in Rice Seedling. In *Information Technology and Agricultural Engineering*; Zhu, E., Sambath, S., Eds.; Springer: Berlin/Heidelberg, Germany, 2012; pp. 881–887. [\[CrossRef\]](#)
116. Srivastava, A.K.; Lokhande, V.H.; Patade, V.Y.; Suprasanna, P.; Sjahril, R.; D'Souza, S.F. Comparative Evaluation of Hydro, Chemo, and Hormonal-Priming Methods for Imparting Salt and PEG Stress Tolerance in Indian Mustard (*Brassicajuncea* L.). *Acta Physiol. Plant.* **2010**, *32*, 1135–1144. [\[CrossRef\]](#)
117. Zhang, F.; Yu, J.; Johnston, C.R.; Wang, Y.; Zhu, K.; Lu, F.; Zhang, Z.; Zou, J. Seed Priming with Polyethylene Glycol Induces Physiological Changes in Sorghum (*Sorghum bicolor* L. Moench) Seedlings under Suboptimal Soil Moisture Environments. *PLoS ONE* **2015**, *10*, e0140620. [\[CrossRef\]](#)
118. Salama, K.H.A.; Mansour, M.M.F.; Hassan, N.S. Choline Priming Improves Salt Tolerance in Wheat (*Triticum aestivum* L.). *Aust. J. Basic Appl. Sci.* **2011**, *5*, 126–132.
119. Azooz, M.M. Salt Stress Mitigation by Seed Priming with Salicylic Acid in Two *Faba Bean* Genotypes Differing in Salt Tolerance. *Int. J. Agric. Biol.* **2009**, *11*, 343–350.
120. Alam, M.U.; Fujita, M.; Nahar, K.; Rahman, A.; Anee, T.I.; Masud, A.A.C.; Amin, A.K.M.R.; Hasanuzzaman, M. Seed Priming Upregulates Antioxidant Defense and Glyoxalase Systems to Conferring Simulated Drought Tolerance in Wheat Seedlings. *Plant Stress* **2022**, *6*, 100120. [\[CrossRef\]](#)
121. Nawaz, A.; Amjad, M.; Jahangir, M.M.; Khan, S.M.; Cui, H.; Hu, J. Induction of Salt Tolerance in Tomato (*Lycopersicon esculentum* Mill.) Seeds through Sand Priming. *Aust. J. Crop Sci.* **2012**, *6*, 1199–1203.
122. Ellouzi, H.; Oueslati, S.; Hessini, K.; Rabhi, M.; Abdelly, C. Seed-Priming with H₂O₂ Alleviates Subsequent Salt Stress by Preventing ROS Production and Amplifying Antioxidant Defense in Cauliflower Seeds and Seedlings. *Sci. Hortic.* **2021**, *288*, 110360. [\[CrossRef\]](#)
123. Ali, Q.; Daud, M.K.; Haider, M.Z.; Ali, S.; Rizwan, M.; Aslam, N.; Noman, A.; Iqbal, N.; Shahzad, F.; Deeba, F.; et al. Seed Priming by Sodium Nitroprusside Improves Salt Tolerance in Wheat (*Triticum aestivum* L.) by Enhancing Physiological and Biochemical Parameters. *Plant Physiol. Biochem.* **2017**, *119*, 50–58. [\[CrossRef\]](#)
124. Dawood, M.G.; El-Awadi, M.E. Alleviation of Salinity Stress on *Vicia faba* Plants via Seed Priming with Melatonin. *Acta Biol. Colomb.* **2015**, *20*, 223–235. [\[CrossRef\]](#)
125. Meena, D.S. Effect of Seed Bio-Priming and N Doses under Varied Soil Type on Nitrogen Use Efficiency (NUE) of Wheat (*Triticum aestivum* L.) under Greenhouse Conditions. *Biocatal. Agric. Biotechnol.* **2016**, *6*, 68–75. [\[CrossRef\]](#)
126. Sen, A.; Johnson, R.; Puthur, J.T. Seed Priming: A Cost-effective Strategy to Impart Abiotic Stress Tolerance. In *Plant Performance Under Environmental Stress Hormones, Biostimulants and Sustainable Plant Growth Management*; Husen, A., Ed.; Springer: Cham, Switzerland, 2021; pp. 459–480. [\[CrossRef\]](#)
127. Zhang, Y.; Zhou, X.; Dong, Y.; Zhang, F.; He, Q.; Chen, J.; Zhu, S.; Zhao, T. Seed Priming with Melatonin Improves Salt Tolerance in Cotton through Regulating Photosynthesis, Scavenging Reactive Oxygen Species and Coordinating with Phytohormone Signal Pathways. *Ind. Crops Prod.* **2021**, *169*, 113671. [\[CrossRef\]](#)
128. Dos Santos Araújo, G.; de Oliveira Paula-Marinho, S.; de Paiva Pinheiro, S.K.; de Castro Miguel, E.; de Sousa Lopes, L.; Camelo Marques, E.; de Carvalho, H.H.; Gomes-Filho, E. H₂O₂ Priming Promotes Salt Tolerance in Maize by Protecting Chloroplasts Ultrastructure and Primary Metabolites Modulation. *Plant Sci.* **2021**, *303*, 110774. [\[CrossRef\]](#)
129. Liu, J.; Hasanuzzaman, M.; Wen, H.; Zhang, J.; Peng, T.; Sun, H.; Zhao, Q. High Temperature and Drought Stress Cause Absciscic Acid and Reactive Oxygen Species Accumulation and Suppress Seed Germination Growth in Rice. *Protoplasma* **2019**, *256*, 1217–1227. [\[CrossRef\]](#)
130. Lanteri, S.; Saracco, F.; Kraak, H.L.; Bino, R.J. The Effects of Priming on Nuclear Replication Activity and Germination of Pepper (*Capsicum annuum*) and Tomato (*Lycopersicon esculentum*) Seeds. *Seed Sci. Res.* **1994**, *4*, 81–87. [\[CrossRef\]](#)

131. Ozbingöl, N.; Corbineau, F.; Groot, S.P.C.; Bino, R.J.; Côme, D. Activation of the Cell Cycle in Tomato (*Lycopersicon esculentum* Mill.) Seeds during Osmoconditioning as Related to Temperature and Oxygen. *Ann. Bot.* **1999**, *84*, 245–251. [\[CrossRef\]](#)
132. Bino, R.J.; Vries, J.N.D.; Kraak, H.L.; Pijlen, J.G.V. Flow Cytometric Determination of Nuclear Replication Stages in Tomato Seeds during Priming and Germination. *Ann. Bot.* **1992**, *69*, 231–236. [\[CrossRef\]](#)
133. Sivritepe, H. The Effect of Priming Treatments on the Viability and Accumulation of Chromosomal Damage in Aged Pea Seeds. *Ann. Bot.* **1995**, *75*, 165–171. [\[CrossRef\]](#)
134. Varier, A.; Vari, A.K.; Dadlani, M. The Subcellular Basis of Seed Priming. *Curr. Sci.* **2010**, *99*, 450–456.
135. Sharma, S.N.; Maheshwari, A. Expression Patterns of DNA Repair Genes Associated with Priming Small and Large Chickpea (*Cicer arietinum*) Seeds. *Seed Sci. Technol.* **2015**, *43*, 250–261. [\[CrossRef\]](#)
136. Hussain, S.; Zhu, C.; Huang, J.; Huang, J.; Zhu, L.; Cao, X.; Nanda, S.; Khaskheli, M.A.; Liang, Q.; Kong, Y.; et al. Ethylene Response of Salt Stressed Rice Seedlings Following Ethephon and 1-Methylcyclopropene Seed Priming. *Plant Growth Regul.* **2020**, *92*, 219–231. [\[CrossRef\]](#)
137. Matsunami, M.; Hayashi, H.; Murai-Hatano, M.; Ishikawa-Sakurai, J. Effect of Hydropriming on Germination and Aquaporin Gene Expression in Rice. *Plant Growth Regul.* **2022**, *97*, 263–270. [\[CrossRef\]](#)
138. Chen, K.; Fessehaie, A.; Arora, R. Aquaporin Expression during Seed Osmopriming and Post-Priming Germination in Spinach. *Biol. Plant* **2013**, *57*, 193–198. [\[CrossRef\]](#)
139. Soeda, Y.; Konings, M.C.J.M.; Vorst, O.; van Houwelingen, A.M.M.L.; Stoop, G.M.; Maliepaard, C.A.; Kodde, J.; Bino, R.J.; Groot, S.P.C.; van der Geest, A.H.M. Gene Expression Programs during *Brassica oleracea* Seed Maturation, Osmopriming, and Germination Are Indicators of Progression of the Germination Process and the Stress Tolerance Level. *Plant Physiol.* **2005**, *137*, 354–368. [\[CrossRef\]](#) [\[PubMed\]](#)
140. Chen, S.; Liu, H.; Yangzong, Z.; Gardea-Torresdey, J.L.; White, J.C.; Zhao, L. Seed Priming with Reactive Oxygen Species-Generating Nanoparticles Enhanced Maize Tolerance to Multiple Abiotic Stresses. *Environ. Sci. Technol.* **2023**, *57*, 19932–19941. [\[CrossRef\]](#) [\[PubMed\]](#)
141. Karalija, E.; Demira, A.; Samardžić, J.; Parić, A.; Dahija, S.; Contaldi, F.; Martinelli, F. RNA Sequencing Indicates Gene Expression Changes in *Silene Sendtneri* Seeds after Seed Priming with Silicic Acid. *Genet. Appl.* **2022**, *6*, 79–88. [\[CrossRef\]](#)
142. Buitink, J.; Leger, J.J.; Guisle, I.; Vu, B.L.; Wuillème, S.; Lamirault, G.; Bars, A.L.; Meur, N.L.; Becker, A.; Küster, H.; et al. Transcriptome Profiling Uncovers Metabolic and Regulatory Processes Occurring during the Transition from Desiccation-Sensitive to Desiccation-Tolerant Stages in *Medicago truncatula* Seeds. *Plant J.* **2006**, *47*, 735–750. [\[CrossRef\]](#)
143. Catusse, J.; Meinhard, J.; Job, C.; Strub, J.M.; Fischer, U.; Pestsova, E.; Westhoff, P.; Van Dorsselaer, A.; Job, D. Proteomics Reveals Potential Biomarkers of Seed Vigor in Sugarbeet. *Proteomics* **2011**, *11*, 1569–1580. [\[CrossRef\]](#)
144. Chen, K.; Arora, R. Priming Memory Invokes Seed Stress-Tolerance. *Environ. Exp. Bot.* **2013**, *94*, 33–45. [\[CrossRef\]](#)
145. Gamir, J.; Sánchez-Bel, P.; Flors, V. Molecular and Physiological Stages of Priming: How Plants Prepare for Environmental Challenges. *Plant Cell Rep.* **2014**, *33*, 1935–1949. [\[CrossRef\]](#)
146. Liu, H.; Able, A.J.; Able, J.A. Priming Crops for the Future: Rewiring Stress Memory. *Trends Plant Sci.* **2022**, *27*, 699–716. [\[CrossRef\]](#)
147. Louis, N.; Dhankher, O.P.; Puthur, J.T. Seed Priming Can Enhance and Retain Stress Tolerance in Ensuing Generations by Inducing Epigenetic Changes and Trans-Generational Memory. *Physiol. Plant.* **2023**, *175*, e13881. [\[CrossRef\]](#)
148. Sen, A.; Puthur, J.T. Seed Priming-Induced Physiochemical and Molecular Events in Plants Coupled to Abiotic Stress Tolerance: An Overview. In *Priming-Mediated Stress and Cross-Stress Tolerance in Crop Plants*; Hossain, M.A., Liu, F., Burritt, D.J., Fujita, M., Huang, B., Eds.; Elsevier International Publishing: Amsterdam, The Netherlands, 2020; pp. 303–316. [\[CrossRef\]](#)
149. Hameed, A.; Hussain, T.; Gulzar, S.; Aziz, I.; Gul, B.; Khan, M.A. Salt Tolerance of a Cash Crop Halophyte *Suaeda frutescens*: Biochemical Responses to Salt and Exogenous Chemical Treatments. *Acta Physiol. Plant.* **2012**, *34*, 2331–2340. [\[CrossRef\]](#)
150. Jithesh, M.N.; Prashanth, S.R.; Sivaprakash, K.R.; Parida, A. Monitoring Expression Profiles of Antioxidant Genes to Salinity, Iron, Oxidative, Light and Hyperosmotic Stresses in the Highly Salt Tolerant Grey Mangrove, *Avicennia marina* (Forsk.) Vierh. by mRNA Analysis. *Plant Cell Rep.* **2006**, *25*, 865–876. [\[CrossRef\]](#) [\[PubMed\]](#)
151. Rai-Kalal, P.; Jajoo, A. Priming with Zinc Oxide Nanoparticles Improve Germination and Photosynthetic Performance in Wheat. *Plant Physiol. Biochem.* **2021**, *160*, 341–351. [\[CrossRef\]](#) [\[PubMed\]](#)
152. Habib, N.; Ali, Q.; Ali, S.; Haider, M.Z.; Javed, M.T.; Khalid, M.; Perveen, R.; Alsahli, A.A.; Alyemeni, M.N. Seed Priming with Sodium Nitroprusside and H₂O₂ Confers Better Yield in Wheat Under Salinity: Water Relations, Antioxidative Defense Mechanism and Ion Homeostasis. *J. Plant Growth Regul.* **2021**, *40*, 2433–2453. [\[CrossRef\]](#)
153. Molassiotis, A.; Tanou, G.; Diamantidis, G. NO Says More than ‘YES’ to Salt Tolerance. *Plant Signal. Behav.* **2010**, *5*, 209–212. [\[CrossRef\]](#)
154. Sangwan, P.N.S.; Saini, N.; Joshi, G. The Role of Nitric Oxide in Plants under Salt Stress: A Review. *J. Plant Biol. Crop Res.* **2024**, *7*, 1098.
155. Kataria, S.; Anand, A.; Raipuria, R.K.; Kumar, S.; Jain, M.; Watts, A.; Brestic, M. Magnetopriming Actuates Nitric Oxide Synthesis to Regulate Phytohormones for Improving Germination of Soybean Seeds under Salt Stress. *Cells* **2022**, *11*, 2174. [\[CrossRef\]](#)

156. Kataria, S.; Jain, M.; Tripathi, D.K.; Singh, V.P. Involvement of Nitrate Reductase-Dependent Nitric Oxide Production in Magnetopriming-Induced Salt Tolerance in Soybean. *Physiol. Plant.* **2020**, *168*, 422–436. [[CrossRef](#)]
157. Wright, B.; Rowse, H.; Whipps, J.M. Microbial Population Dynamics on Seeds during Drum and Steeping Priming. *Plant Soil* **2003**, *255*, 631–640. [[CrossRef](#)]
158. Butler, L.H.; Hay, F.R.; Ellis, R.H.; Smith, R.D.; Murray, T.B. Priming and Re-Drying Improve the Survival of Mature Seeds of *Digitalis Purpurea* during Storage. *Ann. Bot.* **2009**, *103*, 1261–1270. [[CrossRef](#)]
159. Chiu, K.Y.; Chen, C.L.; Sung, J.M. Effect of Priming Temperature on Storability of Primed Sh-2 Sweet Corn Seed. *Crop Sci.* **2002**, *42*, 1996–2003. [[CrossRef](#)]
160. Hill, H.J.; Cunningham, J.D.; Bradford, K.J.; Taylor, A.G. Primed Lettuce Seeds Exhibit Increased Sensitivity to Moisture Content During Controlled Deterioration. *HortScience* **2007**, *42*, 1436–1439. [[CrossRef](#)]
161. Hacısalıhoğlu, G.; Paine, D.H.; Hilderbrand, M.B.; Khan, A.A.; Taylor, A.G. Embryo Elongation and Germination Rates as Sensitive Indicators of Lettuce Seed Quality: Priming and Aging Studies. *HortScience* **1999**, *34*, 1240–1243. [[CrossRef](#)]
162. Ma, H.Y.; Zhao, D.D.; Ning, Q.R.; Wei, J.P.; Li, Y.; Wang, M.M.; Liu, X.L.; Jiang, C.J.; Liang, Z.W. A Multi-Year Beneficial Effect of Seed Priming with Gibberellic Acid-3 (GA₃) on Plant Growth and Production in a Perennial Grass, *Leymus chinensis*. *Sci. Rep.* **2018**, *8*, 13214. [[CrossRef](#)]
163. Hussain, S.; Zheng, M.; Khan, F.; Khaliq, A.; Fahad, S.; Peng, S.; Huang, J.; Cui, K.; Nie, L. Benefits of Rice Seed Priming are Offset Permanently by Prolonged Storage and the Storage Conditions. *Sci. Rep.* **2015**, *5*, 8101. [[CrossRef](#)]

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